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Sexual bimodality in some recent pig populations and application of the findings to the study of fossils

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Abstract

Studied the size differences in some skull and tooth measurements between males and females in recent Suidae.

In three populations of *Sus* the linear measurements of the cheek teeth of the females ($0 \leq n \leq 25$) are on average 97 % those of the males ($0 \leq n \leq 28$). There is much overlap between the sexes. In *Babyrousa* such size differences are of the same order of magnitude. In an earlier study, using skull length, greater differences between the sexes were found. The value of skull length and some other skull measurements is discussed. Male Suidae have larger diastemas and longer skulls because of their larger canines.

The results of this study are applied to a sample of fossil *Bunolistriodon* from Córcoles (Guadalajara, Spain). The material is morphologically homogeneous, but there are two size groups differing on average by 15 %. There is no overlap between the groups. It is concluded that it is more likely that the material from Córcoles represents two species rather than males and females of the same species.

Introduction

A morphologically homogeneous collection of *Bunolistriodon* fossils from the Lower Miocene locality of Córcoles (Guadalajara, Spain) consists of two size groups, differing by 15 %. The question arose whether these groups represent two species or males and females of the same species. Usually sexual dimorphism in Suidae is apparent in the canines, but this criterion could not be used due to the state of preservation of the fossils. The present dilemma is not an isolated one in the study of fossil pigs (Pickford and Wilkinson 1975).

In some families sympatric morphologically similar species differ in size by 15 % (recent peccaries: Rusconi 1929; *Dorcatherium:* Mottl 1961; Fahlbusch 1985), whereas in other families males and females of one species differ by up to 13 % (Ursidae: Kurtén 1969; Torres 1984).

This paper deals with the size differences between males and females in recent pigs. The cheek teeth were measured as it is the intention to apply the findings to the study of fossils. In addition some skull measurements were taken.

Material and methods

Three collections of recent species, in which the canines indicate the sex of the specimen are studied. These collections represent approximately three populations, because they were made in a small area during a relatively short time. Not all measurements could be taken in all skulls, because of teeth that are not yet erupted or because of damage. The number of measurements taken are given in the tables.

The largest population measured is one of *Sus scrofa vittatus* from the former residence Deli, Sumatra, now called Sumatera Utara. The collection is stored in the Zoological Museum of Amsterdam (ZMA). The lower cheek teeth were measured and several skull measurements were taken. Males and females are about equally represented. The males are on average younger, in many the M_3 is not yet erupted or the talonid is still partly covered by bone (such individuals are considered to be subadults).

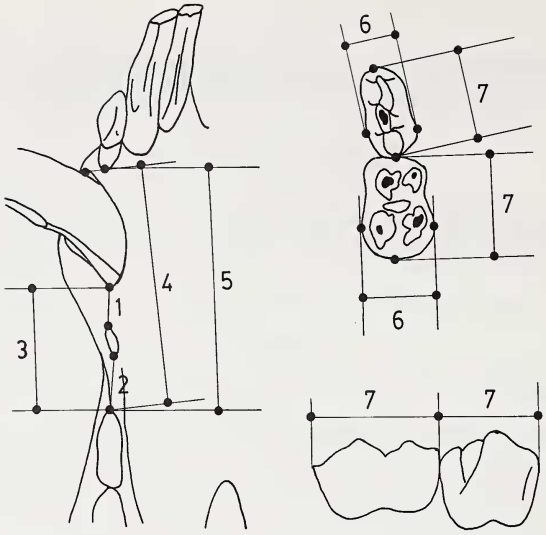

Fig. 1. The way of measuring. Diastemas and distances measured as the shortest distance between alveoli: 1. diastema C–P_1; 2. diastema P_1–P_2; 3. distance C–P_2; 4. distance P_2 – front of canine; 5. distance I_3–P_2; 6. DT, the greatest width (either measured at the anterior or at the posterior lobe) and 7. DAP, the greatest length of a tooth. (Measurements are in mm)

A smaller sample of *Sus barbatus* from east Bulongan, Borneo in the ZMA consists mainly of skulls without mandibles.

Sus verrucosus was measured in the ZMA and at Leyden in the Rijksmuseum voor Natuurlijke Historie (RMNH). Only specimens with a label indicating the provenance of Java were used. The females are underrepresented. No attempt has been made to measure all male material, which is very abundant. Most of the females of this species in the RMNH, also those which do not have a label specifying the provenance, do not have a fully erupted M_3. But most of the males are fully adult.

In addition data on recent *Babyrousa* from Bumbulan (females $3 \leq n \leq 5$, males $12 \leq n \leq 13$) and Buru (females $2 \leq n \leq 3$, males $13 \leq n \leq 16$) were taken from Groves (1980).

The fossil *Bunolistriodon* material ($0 \leq n \leq 5$) will be compared to the recent material. It is stored in the geology department of the Universidad Complutense in Madrid and it is under study by V. d. Made and Alférez.

Measurements of diastemas and the length of the skull are given for *Sus scrofa* only, as it is the largest sample.

Length and width of the cheek teeth and length of diastemas were measured as indicated in figure 1. Skull length was measured in the median plane from the tip of the nasalia to the posterior edge of the occiput. All measurements are in mm.

The value Q is introduced to express the mean size of a character of the females relative to the mean size of the males. It is given as a percentage. Q = (mean females/mean males) × 100 %.

Results

Average lengths and widths of the cheek teeth of *Sus* are given in table 1. On average females appear to be only slightly smaller than the males. Q values show little variation in the large *Sus scrofa* sample ($92 \leq Q \leq 101$), the average value is 97. Q values in the *Sus verrucosus* sample show more variation ($88 \leq Q \leq 123$), the average value is 98. The average Q value for *Sus barbatus* is 97 ($87 \leq Q \leq 105$), for *Babyrousa* from Buru 95 ($93 \leq Q \leq 99$) and for *Babyrousa* from Bumbulan 101 ($94 \leq Q \leq 106$). The average Q value for all populations is 98. Although the only sample in which females are well represented is that of *S. scrofa*, it is striking that in none of the other samples the average Q

Table 1. **Average dimensions of the cheek teeth of *Sus***
DAP = greatest length; DT = greatest width; n = number of measurements taken. Measurements in mm

	P_1 Mean	n	P_2 Mean	n	P_3 Mean	n	P_4 Mean	n	M_1 Mean	n	M_2 Mean	n	M_3 Mean	n
Sus scrofa vittatus														
DAP females	7.7	11	11.1	24	12.2	24	13.3	25	14.9	11	19.1	23	32.9	17
DAP males	7.6	10	11.3	19	12.8	25	14.2	27	15.2	25	19.9	28	34.0	11
DT females	3.8	10	5.6	24	7.4	24	9.3	25	10.8	11	14.3	23	16.2	17
DT males	3.8	11	5.8	19	7.6	25	10.1	27	10.8	25	14.7	28	16.6	11
Sus verrucosus														
DAP females	7.6	1	10.0	1	13.3	2	15.8	3	16.2	3	22.2	3	39.0	1
DAP males	6.2	7	11.4	8	13.9	8	15.1	8	15.2	8	21.5	8	40.8	5
DT females	3.0	1	5.4	1	6.9	2	10.0	3	10.7	3	13.9	3	16.1	2
DT males	3.0	7	6.0	8	7.2	8	9.8	8	11.0	8	14.6	8	18.1	6
Sus barbatus														
DAP females					14.7	1	14.9	2	17.6	2	23.1	2		
DAP males					14.7	7	15.5	6	18.0	5	24.0	6		
DT females					7.7	1	9.7	2	13.2	2	15.4	2		
DT males					7.6	7	10.2	6	12.6	5	16.6	6		

	P^1 Mean	n	P^2 Mean	n	P^3 Mean	n	P^4 Mean	n	M^1 Mean	n	M^2 Mean	n	M^3 Mean	n
Sus verrucosus														
DAP females	8.0	2	11.9	2	13.4	3	12.5	3	16.0	3	22.4	3	34.0	1
DAP males	8.6	6	12.4	7	13.0	8	12.5	8	15.7	7	22.0	8	35.7	6
DT females	3.6	2	6.8	2	10.4	3	13.3	3	12.8	3	16.6	3	18.5	2
DT males	3.6	6	7.6	7	11.1	7	13.5	8	13.3	7	17.4	8	19.9	6
Sus barbatus														
DAP females			12.7	2	12.9	4	12.8	6	17.7	5	22.8	6	35.6	3
DAP males			13.5	6	13.5	7	13.1	7	18.2	6	24.5	7	34.7	4
DTR females			7.7	2	11.4	5	14.4	6	15.1	5	18.4	7	20.4	3
DT males			8.9	6	12.0	7	14.5	7	15.5	6	19.4	7	21.0	4

Table 2. **Dimensions of the diastemas and skull lengths (in mm) of *Sus scrofa vittatus***

		Distance					
		$P_1 - C$	$P_1 - P_2$	$C - P_2$	Front $C - P_2$	$I_3 - P_2$	Skull length
Subadult	minimum	1.4	0.0	9.9	23.1	23.6	257
(n = 7)	mean	3.0	2.9	13.5	25.0	27.6	275
	maximum	5.1	5.1	16.8	27.3	31.2	295
Adult females	minimum	0.6	0.0	9.2	13.0	24.9	270
($14 \leq n \leq 17$)	mean	3.5	2.1	13.3	25.0	29.0	297
	maximum	6.1	7.3	20.1	31.5	35.2	321
Subadult	minimum	4.6	1.0	13.9	25.2	28.2	277
($12 \leq n \leq 14$)	mean	6.0	3.8	17.6	31.6	32.5	298
	maximum	8.1	6.4	22.1	38.3	39.2	321
Adult males	minimum	0.0	1.0	13.9	27.9	33.6	299
($8 \leq n \leq 12$)	mean	5.3	5.6	18.7	37.5	37.4	320
	maximum	7.8	12.7	22.9	44.0	40.8	342
Means							
100 × (subadult males/adult males)		113	68	94	84	87	93
100 × (subadult fem./adult fem.)		86	138	102	100	95	93
Q subadults		50	76	77	79	85	92
Q adults		66	38	71	67	78	93

value differs much from the value of this sample. The smaller size group in the *Bunolistriodon* material averages 85 % of the larger size group.

Size overlap between the sexes of *Sus scrofa vittatus* is great, in none of the cheek teeth two concentrations are formed (figure 2). This is also the case in *Sus verrucosus* and *Sus barbatus*. The size groups are better separated in similar diagrams for *Bunolistriodon*.

The size of the diastemas is about twice as large in the males as in the females (table 2). Also the total distance between the last incisor and the P_2 is much larger. In a similar way subadults of each sex have lower values than the adults, although there are some exceptions.

The Q value for skull length is 94 % (table 2).

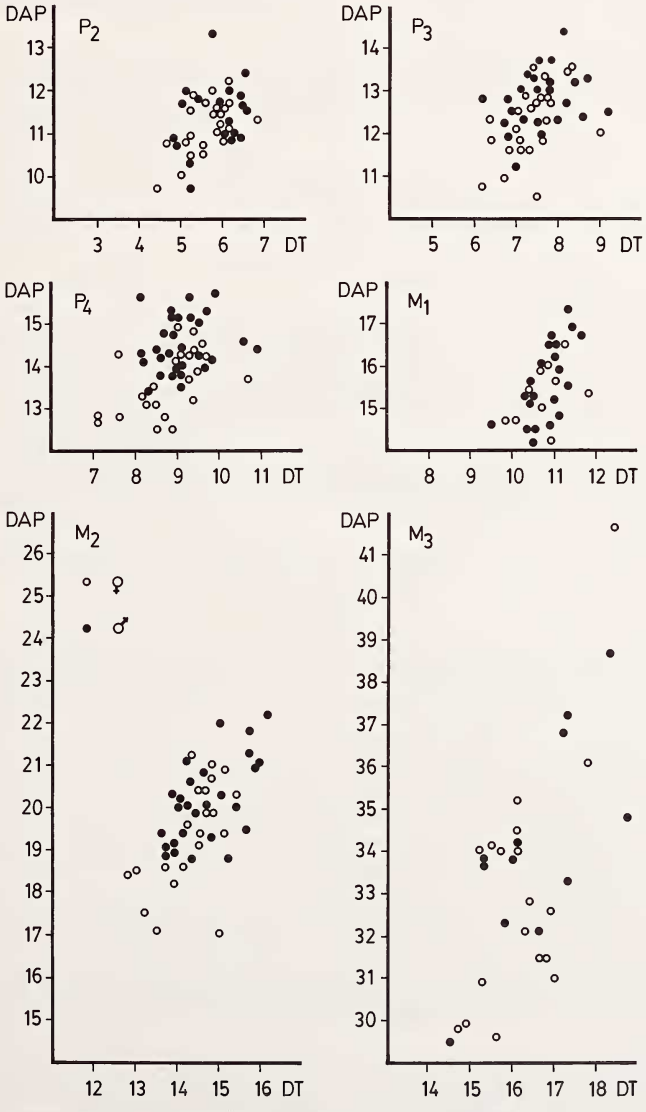

Fig. 2. Scatter diagrams for *Sus scrofa vittatus* from Deli. In the diagram for the M_3 a particularly large molar of which the complete width could not be measured is also given. (Measurements are in mm)

Discussion

The cheek teeth in *Sus scrofa* females are 97 % the size of the cheek teeth in the males. As the smaller samples do not differ in a substantial way (their average Q values vary from 95 to 101) the value of 97 % seems to be representative for the cheek teeth.

Average size differences between the sexes of 3 % only, seem to contradict the findings of Groves (1981). He found that females averaged 85.4–95.3 of the males, 80.8–83.3 in *Sus verrucosus*. Groves' values are based on the condylobasal lengths of the skulls. These measurements are roughly comparable to the skull length as measured in this study. The skull length includes the part with the canines; these zones are highly sexually dimorphic. The large *Sus scrofa* sample will be used to show how sexual dimorphism in the canine area causes a bimodality in skull lengths.

In the Deli sample the mean distance between I_3 and P_2 is 8.4 mm greater in the adult males than in the adult females; the difference for the skull length is 23 mm. If the males had no enlarged canines and diastemas their skulls would have an average length of 312 mm. The average female skull measures 297, which is 95 % of 312 mm. The dentition indicates a value of 97 %. So a large part of the size difference in female and male skulls is accounted for by the large canine zone in the males. In *S. verrucosus* diastemas tend to be much longer than in *S. scrofa* and in the small *S. verrucosus* sample size differences of the P_2–I_3 distance is 22.8 mm, which is much greater than in *S. scrofa*. So, a greater sexual bimodality in skull length is to be expected in *S. verrucosus,* although size differences in cheek teeth are not greater than in *S. scrofa*.

Part of the size difference for *Sus verrucosus* found by Groves (1981) might be explained in this way, but the difference in length of the M_3 for *S. verrucosus verrucosus,* as listed by him, is large: females average 86 % of the males. My measurements indicate 96 % for the length of the M_3. There is no explanation for this discrepancy. It should be noted that for *S. verrucosus blouchi* the same value is 95 %. Also the standard deviation for the M_3 of the females of *S. v. verrucosus,* as given by Groves (1981), is large. In any case, if an indication of size is needed for taxonomical purposes it is advisable to use a measurement that is less variable than skull length.

Sexually dimorphic canines influence both skull length and diastema length. Diastema length is used by some authors for taxonomical purposes (Thenius 1972).

The difference in size of the diastemas in the females and males is related to the size of the canines. The larger the upper canines the larger are the diastemas behind the lower canines, and the same reasoning applies to the lower canines and the diastemas in front of the upper canines. As the canines of the males keep on growing (also their antero-posterior and transverse diameters increase) the diastemas have to grow too: the subadult/adult values for the distances C–P_2, front of canine – P_2 and I_3–P_2 are lower in the males than in the females (table 2). The continued size increase of the canines in the males seems to cause a decrease of the C–P_1 and C–I_3 distances, indicating that bone of the mandible is resorbed. The subadult/adult ratio for the P_1–P_2 (too high) and P_1–C (low) distances in the females is caused by a large number P_1 in contact with the P_2 in the adult females. The position of the P_1 seems to be variable.

The value of the size of the diastemas for taxonomy is restricted, as this character is related to sex and age and is influenced by the variable position of the P_1. If it is necessary to indicate the size of diastemas, it seems better to give the distance I3–P2 or the distance from the front of the canine to the P_2 in the mandible or the distance from the P^1 to the I^3 or I^2 in the upper jaw.

In the studied species the size difference between the males and females is small; in their direct ancestors this is probably also the case. Species of other subfamilies than Suinae are only known as fossils, so a study of this kind can be done for the Suinae only. The fact that size variation in large fossil samples is not greater than in recent species is an indirect

indication that large size differences between the sexes in fossil Suidae do not occur. Size variation in Suoidea will be subject to a separate study. Scanty fossil material of which the sex is known also indicates that there are no great size differences between females and males.

The presence of two species of *Bunolistriodon* in Córcoles instead of merely two sexes of one species, is likely because of:

1. The average size difference between the two size groups in *Bunolistriodon* from Córcoles is 15 %, which is much more than the 3 % of average size difference found in recent male and female Suidae.
2. The size groups are separated and do not have a large overlap as males and females of extant species.

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Zusammenfassung

Geschlechtsbimodalität bei einigen rezenten Schweinepopulationen und Anwendung der Befunde für das Studium an Fossilien

Diese Studie beschäftigt sich mit den Größenunterschieden zwischen weiblichen und männlichen Schweinen. In drei rezenten Populationen von *Sus* betragen die linearen Maße der Backenzähne der Weibchen ($0 \leq n \leq 25$) durchschnittlich 97 % derjenigen von Männchen ($0 \leq n \leq 28$). Bei *Babyrousa* liegen die Unterschiede in gleicher Größenordnung.

In einer früheren Untersuchung wurden bei Bezug auf die Schädellänge größere Unterschiede zwischen den Geschlechtern gefunden. Diese Studie stellt den Wert von Schädellängenmessungen und anderen Maßen zur Diskussion. Männliche Suidae haben längere Diastemen und längere Schädel wegen ihrer größeren Caninen.

Die Ergebnisse dieser Studie wurden auf eine Probe von Fossilen *Bunolistriodon* von Córcoles (Guadalajara, Spanien) angewandt. Dieses Material ist morphologisch homogen, aber in bezug auf die Größe können zwei Gruppen unterschieden werden. Der Unterschied beträgt 15 %, und es gibt keine Überschneidungen. Daraus wird geschlossen, daß das Material von Córcoles eher zwei Arten repräsentiert als die Geschlechter derselben Art.

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